

A new species of genus *Provanna* (Gastropoda, Abysochrysoidea) from gas hydrate-bearing sediments of the northern South China Sea

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Abstract

The genus *Provanna* (belonging to Superfamily Abysochrysoidea) is a group of globally distributed gastropods commonly discovered in the deep-sea chemosynthetic environments. To date it is composed of 29 extant and nine fossil species and all of them seem to be endemic to vents, seeps or organic falls. Despite the increasing interest in cold seeps in South China Sea in recent decades, how this genus is distributed in this area is largely unknown. A new fossil species, *Provanna dongshaensis* **sp. nov.**, collected from the hydrate-bearing sediments in the cold seep area of northern SCS, was studied. A basic morphological description together with the observation of shell microstructures was made, and a brief comparison to known *Provanna* species was summarized. The occurrence depths of this new species are consistent with the remarkable negative carbon isotope of carbonate layers, which mutually supports the relationship to the ancient seep. Such sedimentary samples from drilling cores may be potentially better materials for systematic research of deep-sea gastropods and other chemosynthesis fauna.

Key Words

Ancient seep, fossil, *Provanna*, South China Sea

Introduction

Provanna is a genus of small gastropods found in deep-sea chemosynthetic communities such as hydrothermal vents, hydrocarbon seeps, and organic falls like sunken wood and whale falls. They are known to primarily feed on bacterial mats and detritus, functioning as both deposit feeders and grazers (Warén and Bouchet 1986, 1993; Sibuet and Olu 1998; Sasaki et al. 2010).

The genus *Provanna* is considered the most diverse among the superfamily Abysochrysoidea (Johnson et al. 2010), encompassing 29 extant species (Chen et al. 2016a, 2019; Betters and Cordes 2023) and nine fossil

species (Amano and Jenkins 2013; Amano and Little 2014). The extant species have been identified in various deep-sea environments globally, including West Pacific (Okutani 1990; Okutani et al. 1992; Okutani and Fujikura 2002; Sasaki et al. 2016; Chen et al. 2016a, 2019; Ogura et al. 2018; Chen and Watanabe 2022), Fiji (Warén and Bouchet 1993), the East Pacific (Warén and Bouchet 1986, 1989), the Gulf of Mexico (Warén and Ponder 1991), the Caribbean Sea, the Southern Ocean (Linse et al. 2019), and West Africa (Warén and Bouchet 2009). On the other hand, fossil species have primarily been found in hydrocarbon seep deposits in Japan (Kaim et al. 2008, 2009; Amano and Jenkins 2013; Amano and Little

2014), the USA (Kiel 2006; Hybertsen and Kiel 2018), Peru (Kiel et al. 2020), Trinidad (Gill et al. 2005; Kiel and Hansen 2015) and New Zealand (Saether et al. 2010). Notably, there appears to be a prevalent peri-Pacific distribution pattern for the genus *Provanna*, with a concentration around Japan and the east coast of the USA, except for seven specific localities in the Gulf of Mexico, West Africa, the Caribbean Sea, Trinidad, and the East Scotia Ridge (Fig. 1). Nevertheless, recent years have witnessed a rise in more definitive discoveries of *Provanna* species in additional typical seep regions like West Africa and the Southern Ocean (Saether et al. 2010; Amano and Jenkins 2013; Amano and Little 2014; Sasaki et al. 2016; Hybertsen and Kiel 2018; Linse et al. 2019; Kiel et al. 2020). Since 2010, 15 *Provanna* species, comprising nine extant and six fossil species, have been formally described, representing one-third and two-thirds of the extant and fossil groups, respectively. Betters and Cordes (2023) extends the distribution range of *P. laevis*, *P. ios*, and *P. pacifica*, and presents a comprehensive review of the genus *Provanna*, integrating the geographic distribution, genetics, and morphological characteristics of each extant species. Despite these developments, the global biodiversity of the genus *Provanna* remains inadequately documented.

In the South China Sea (SCS), a marginal sea of the Pacific Ocean, seep carbonates were first discovered in the northern SCS in 2004 (Chen et al. 2005). Since then, several sites of hydrocarbon seepage have been identified, indicating the presence of cold seep systems in the region (Feng et al. 2018). However, limited attention has been given to the gastropods related to the chemosynthetic system in this area, with scant information available on the detailed taxonomy and distribution of the genus *Provanna* in the South China Sea.

During China's second gas hydrate drilling expedition (GMGS-2) in the east of the Pearl River Mouth Basin, SCS, long drilling core sediments containing carbonate deposits were obtained. This acquisition gave a chance to investigate the local chemosynthetic community with a special emphasis on animals that have carbonate shells. Several specimens of the provannid genus were fortunately retrieved from the hydrate-bearing layers and have been identified as a new type within the genus *Provanna*. In this study, we give a formal description of the specimens, together with observations of their shell microstructures. Additionally, we undertake some brief comparisons with other *Provanna* species, and explain the geological significance of this newly found species.

Material and methods

Specimens of the new fossil *Provanna* were discovered in two drilling sites, GMGS2-07B and GMGS2-09B, at a water depth of 791 m and 664 m respectively, located in Dongsha area, northern part of SCS (Fig. 1 with a window partial magnified).

The individual gastropods were collected after the treatment of sediment sample by soaking and screening, a similar laboratorial processing of the coarse fraction analysis. 16 to 40 grams of dried sediment for each sample was soaked for 2 days in the beaker without any chemical dispersing agent until completely dispersed. It was then washed through a 250-mesh copper screen (pore size = 0.063mm), until each sample was guaranteed to be clean. For each specimen, the sampling procedure is as follows: (1) Sectioning is performed along the axis from the apex to the umbilicus of the shell. This results in two cross-sections.

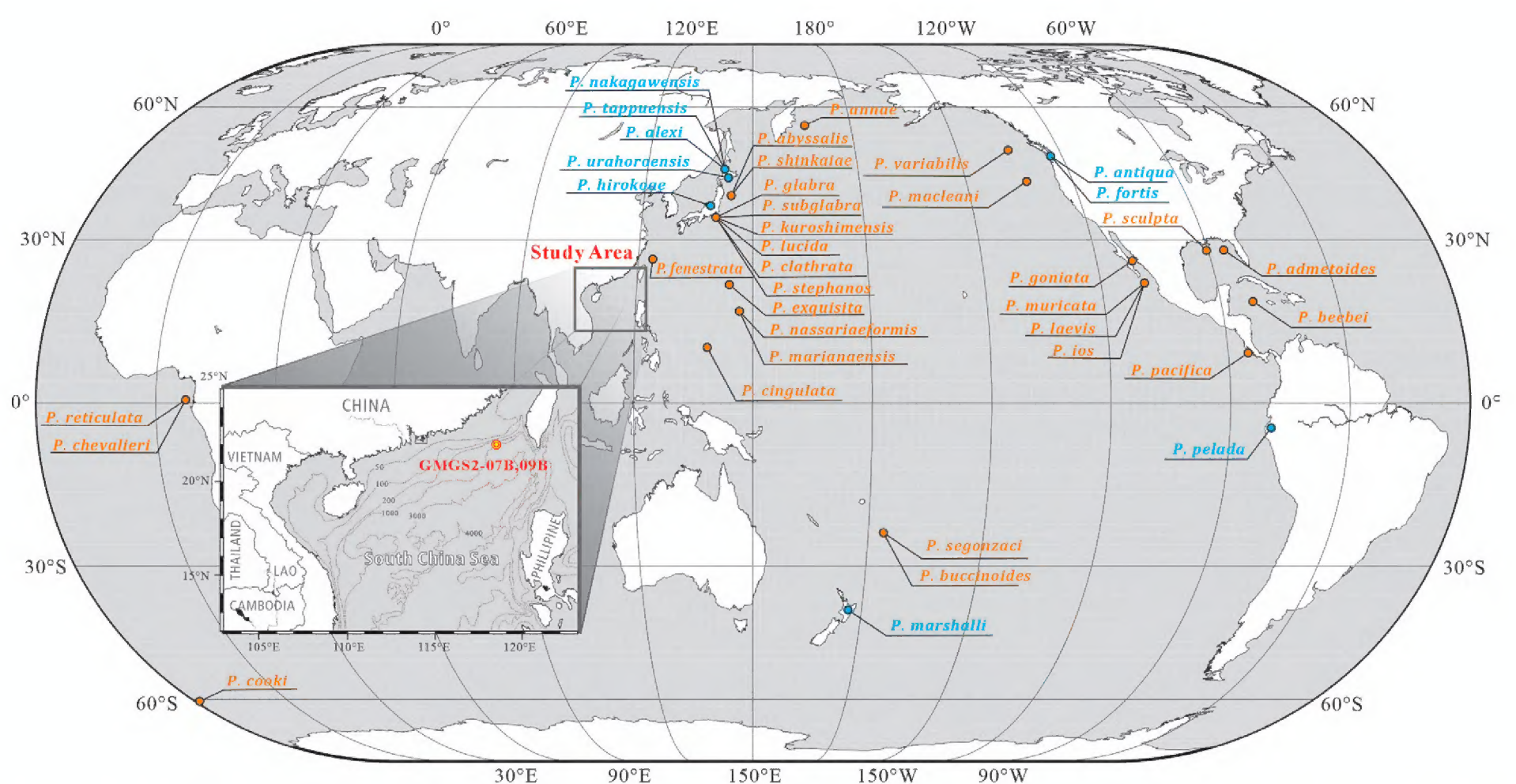


Figure 1. Global distribution of genus *Provanna* displayed as type locations of known species and location of this study (GMGS2-07B and GMGS2-09B). orange circle: active hydrothermal vents, hydrocarbon seeps where extant *Provanna* species are discovered; blue circle: seep deposits or organic falls that yield fossil *Provanna*.

tions of the shell; (2) Sampling is conducted at intervals of 1 cm from the apex, with each sample measuring approximately 1 cm×1 cm; (3) The sectioned shells are polished on sandpapers with grit sizes of 220, 600, 800, 1200, 2000, and 3000 for a duration of 3 minutes each; (4) After each polishing step, the specimens are cleaned in an ultrasonic cleaner for 15 seconds; (5) The polished samples are then immersed in an EDTA solution buffered with ammonia to a pH of approximately 7–8, with a small amount of formaldehyde added, for a period of 10 minutes; (6) The samples, after immersion, are cleaned in an ultrasonic cleaner for two cycles of 20 seconds each; (7) The samples are then air-dried in a cool, dry place for 48 hours; (8) The shell quality structure is initially observed under a microscope to assess clarity; if the structure is clearly visible, the process proceeds to the next step, otherwise, steps (3)–(8) are repeated. Morphological observation and morphometric measurements of the shell were carried out under a Zeiss Discovery V20 stereo microscope. Scanning electron microscopy (SEM) of these specimens were carried out uncoated at 15 kV in a Hitachi TM3030 SEM provided by Guangzhou Marine Geological Survey (GMGS).

Systematic description

Clade Caenogastropoda Cox, 1960

Superfamily Abyssochrysoidea Tomlin, 1927

Family Provannidae Warén & Ponder, 1991

Genus *Provanna* Dall, 1918

Type species. *Trichotropis (Provanna) lomana* Dall, 1918; Magdalena Bay, USA, Recent.

***Provanna dongshaensis* sp. nov.**

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Fig. 2A–O

Etymology. This new species is the only appearance of genus *Provanna* in SCS to date. We use the specific epithet “dongsha” to present the place where it is discovered.

Type material. *Holotype*: GMGS2-09B-C15-2. *Paratype*: GMGS2-07B-A1.

Type locality. Site GMGS2-07B, GMGS2-09B, Dongsha area, northern SCS (Fig. 1).

Buried depth and type horizon. 3.50, 3.60, 6.07 mbsf (meter below sea floor) at core GMGS2-09B, 33.85 mbsf at core GMGS2-07B; Carbonate layers, Late Pleistocene (Table 1).

Material. Type material and other fragment specimens. All specimens are deposited in China Deep Sea Drilling Core Repository, Guangzhou City, China.

Dimensions. Holotype is approximately 7.80 mm in height and 5.02 mm in width of the whole whorl, 3.66 mm in apertural height and up to 0.58 mm thick at the apertural wall. Apical angle of approximately 54° reaching at least 3.66 mm in height and 3.02 mm in width.

Diagnosis. A medium-sized *Provanna*, sturdy, shell with prominent, angular whorls with nodes at intersection of the axial and spiral ribs.

Description. Protoconch: at least one whorl, but poor preservation in all specimens; maximum diameter about 0.58 mm (Fig. 2C); sculptured pattern not clear; transition to teleoconch unknown. Teleoconch: shell height 7.8 to more than 10 mm. Diameter of the last whorl 5.02 to 7.13 mm. Shell thick, 0.41 to 0.58 mm in the thickness of last whorl. Shell four to five whorls, sculptured by reticulate pattern. 15 to 16 strongly orthocone axial ribs (Fig. 2C, H, L) on both the penultimate and last whorls. Three prominent and equally strong spiral ribs with blunt, strong and swollen tubercles at intersections on the penultimate whorl, and up to 7 on the last whorl. Tubercles more prominent on lower whorls, like strings of pearls. Basal margin marked by the distinct with strength-decreasing spiral rib. Axial ribs start at the upper suture and fade below the lower spiral rib. Regularly and closely spaced, fine spiral treads on whorl flank, fine axial growth increments. Aperture broadly oval, siphonal canal bordered by low ridge.

Remarks. (Table 2) *P. dongshaensis* sp. nov. is differentiated from those provannids with smooth shell surface and simple sculpture by its prominent angulate appearance, particularly including the extant species living in Japan seeps and vents (e.g., *P. abyssalis*, *P. glabra*, also see “Shell microstructures of *Provanna*”). It exhibits a smaller number of the spiral ribs but more pronounced axial structure compared to *P. cingulata* and *P. macleani*. *P. dongshaensis* sp. nov. shares with *P. sculpta* the strong and inflated tubercles, which makes them different from those spiny species like *P. goniata*, *P. ios*, *P. stephanos*, etc, but differs in its shelf-structure. Compared to another similar species, *P. fortis*, it has more robust axial structures on the body-whorl, which are generating the inflated tubercles and bead-like appearance.

Stratigraphic and geographic range. Only from the type locality and horizon.

Discussion

Morphological comparison within genus

Provanna

The shell-shape characteristics can be used for the rapid identification of *Provanna*, particularly in fossil materials that lack organic body. Certain characteristics unify all *Provanna* species and distinguish the genus. Their specimens are never wider than tall. Regardless of their size, the specimens typically feature no more than 2 to 3 unbroken shell whorls, thin periostracum, no umbilicus, and small, turbinate, dextral shells. Their apertures have a characteristic shape, rarely being circular or ovate. Betters and Cordes (2023) conducted a comprehensive taxonomic review of extant species and a new identification key for this genus based on their shell and radular morphology, providing an effective method to streamline and standardize species identifications.

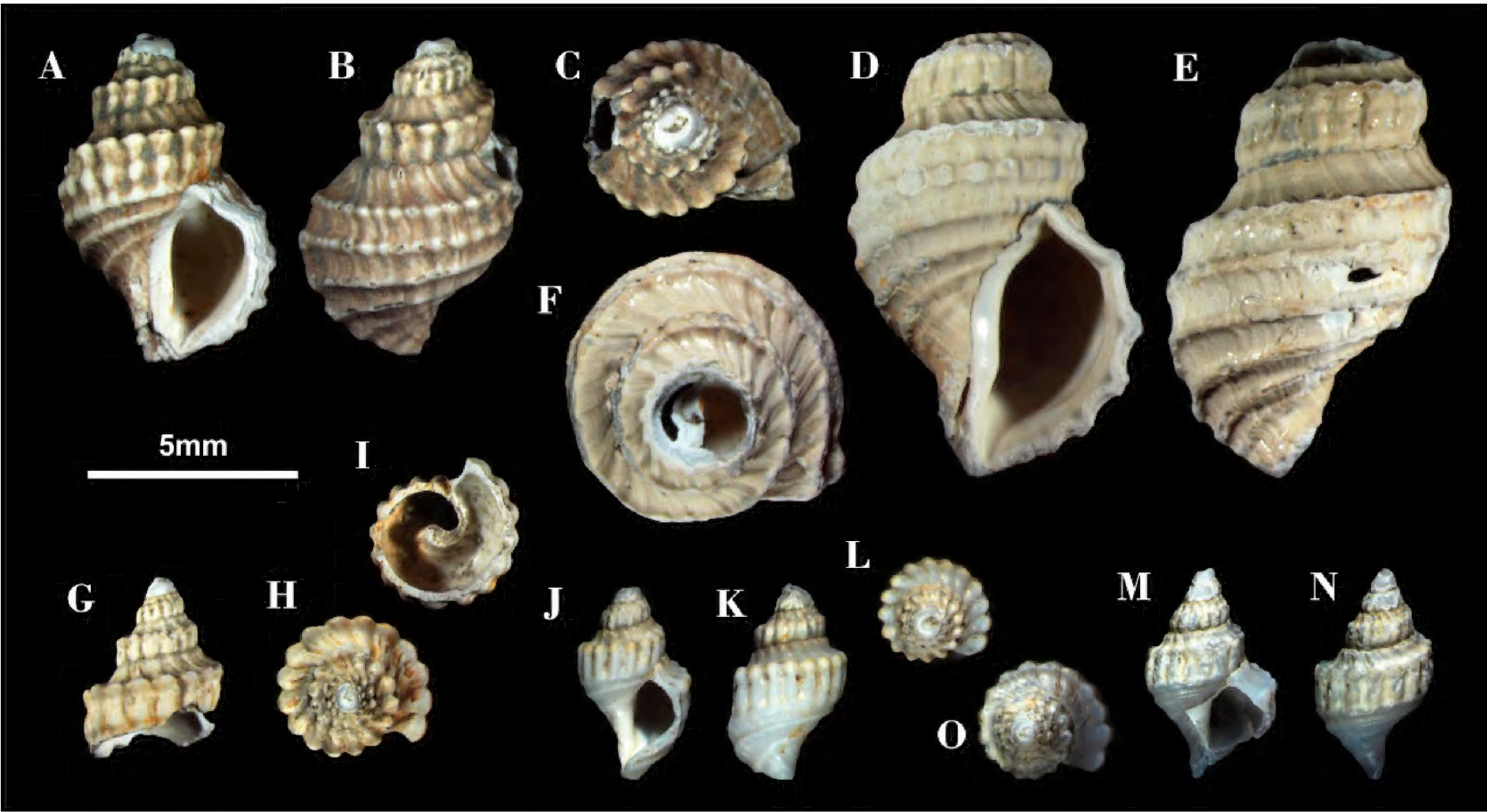


Figure 2. *Provanna dongshaensis* sp. nov., from a late Pleistocene seep site in the northern SCS. **A–C.** (Holotype, GMGS2-09B-C15-2). Specimen from core 09B-4, shell height: 7.8mm; **D–F.** (Paratype, GMGS2-07B-A1). Specimen from core 07B-2H-2A with the protoconch almost lost, shell height: 10.89mm; **G–I.** Incomplete specimen GMGS2-09B-C15-1 from core 09B-2M-1A; **J–L.** Incomplete specimen GMGS2-09B-C14 from core 09B-4. **M–O.** Incomplete specimen GMGS2-09B-C13 from core 09B-2M-1A. Scale bar: 5 mm.

Table 1. General information of specimens found in the Site GMGS2-07B and GMGS2-09B.

Specimens No.	Type	Measurements (mm)	Protoconch	Surface preservation	Depth (mbsf)	Sampling core	Ages (a.B.P.)
GMGS2-09B-C15-2 (Fig. 2A–C)	holotype	shell height: 7.80; diameter of the last whorl: 5.02; apertural height: 3.66; shell thickness of the last whorl: 0.58	broken	slightly eroded	6.07	09B-4	16230 ± 50 *
GMGS2-07B-A1 (Fig. 2D–F)	paratype	shell height: >10.89; diameter of the last whorl: 7.13; apertural height: 6.77; shell thickness of the last whorl: 0.41	unknown	strongly eroded	33.85	07B-2H-2A	91693**
GMGS2-09B-C15-1 (Fig. 2G–I)		(fragment)	broken	eroded	3.50	09B-2M-1A	15120 ± 50 *
GMGS2-09B-C14 (Fig. 2J–L)		(fragment)	unknown	strongly eroded	6.07	09B-4	16230 ± 50 *
GMGS2-09B-C13 (Fig. 2M–O)		(fragment)	broken	eroded	3.60	09B-2M-1A	15120 ± 50 *

*: AMS ¹⁴C dating data using associated coral fragments (unpublished).
**: estimated according to the age of FO of *Globigerinoides ruber* (Pink) (0.12 Ma) at the depth of 44.30 mbsf.

Despite the absence of a radula in our material, the polytomous key for species identification by Betters and Cordes (2023) holds significant reference value for distinguishing extant species. Applying Beeters’ method, *P. dongshaensis* sp. nov. appears to have “both axial and spiral sculpturing” and “sculptural elements present,” making it distinctly different from those Provannids with 1) a smooth shell surface, such as *P. abyssalis*, *P. glabra*, *P. kuroshimensis*, *P. laevis*, *P. lucida*, *P. subglabra*, and *P. urahoroensis* (fossil species); 2) only axial or spiral sculpturing, such as *P. chevalieri*, *P. lomana*, and *P. variabilis*.

To facilitate a more in-depth discussion of other complex structural varieties, particularly the differentiation of fossil species, additional essential points regarding the shell, including angulation, tubercles, spiral ribs, and shelf-structure, are consequently elaborated upon here as supplementary remarks to “Remarks.”

Two Miocene fossil species, *P. alexi* and *P. hirokoeae*, inhabited the Japanese seep location described by Amano and Little (2014), which are lacking the angulation, strong axial and spiral sculpture on the body-whorl, although the spiral base has an increasing number of spiral ribs. *P. cingulata*

Table 2. Spatial distribution, geological time, and survival depth (extant species) of all known species of genus *Provanna*, associated with their morphological comparisons to the *Provanna dongshaensis* sp. nov. described in this study.

Species of <i>Provanna</i>	Distribution and Environment	Buried/survival depth (m)	Ocean/Area*	Age	Morphological comparison to <i>P. dongshaensis</i> sp. nov.
† <i>P. alexi</i> Amano & Little, 2014	Shosanbetsu Village, northwestern Hokkaido, Japan, Chikubetsu Formation, whale-fall.	–	WP	Miocene	lack the strong angulation
† <i>P. antiqua</i> Squires, 1995	Washington State, USA, seep and wood-fall.	–	EP	Eocene to Oligocene	rounded whorls and lacks spines/tubercles
† <i>P. fortis</i> Hybertsen & Kiel, 2018	Satsop Weatherwax seep deposit, Washington State, USA.	–	EP	Eocene	the most similar, 4–5 whorls, distinct angulation, 2 spiral ribs on the spiral base and up to 5 on the lowermost whorl, the same shelf-structure with new type, but less distinct strong axial structure, which make the new type a new species
† <i>P. hirokoe</i> Amano & Little, 2014	Joetsu City, Niigata, Japan, Ogaya Formation, seep.	–	WP	Miocene	lack the strong angulation
† <i>P. marshalli</i> Saether, Little & Campbell, 2010	East Coast Basin, North Island, New Zealand, Bexhaven and Ihungia Limestone Formation, seep.	–	WP	Miocene	similar to <i>P. antiqua</i> , lacks strong angulation but more spiral ribs on the whorls than <i>P. dongshaensis</i> sp. nov.
† <i>P. nakagawaensis</i> Kaim, Jenkins & Hikida, 2009	Nakagawa area, northwestern Hokkaido, Yezo Group, seep and wood-fall.	–	WP	Cretaceous	a distinct reticulate pattern, lacks the spines and does not have the shelf-structure made up by strong angulation
† <i>P. pelada</i> Kiel et al., 2020	Cerros El Pelado block 2, Talara Basin, Peru.	–	SA	Oligocene	–
† <i>P. tappuensis</i> Kaim, Jenkins & Warren, 2008	Tappu area, northwestern Hokkaido, Japan, Yezo Group, seep.	–	WP	Cretaceous	strong axial and spiral sculpture, but less spiral ribs on the body-whorl
† <i>P. urahoroensis</i> Amano & Jenkins, 2013	Uraho, eastern Hokkaido, Japan, Nuibetsu Formation, seep.	–	WP	Oligocene	does not have the distinct reticulate pattern or anything resembling the spines
<i>P. dongshaensis</i> sp. nov. (this study)	Dongsha area, northern South China Sea, seep.	–	WP	Late Pleistocene	–
<i>P. abyssalis</i> Okutani & Fujikura, 2002	Japan Trench, seep.	5379	WP	Recent	rounded whorls and lacks spines/tubercles
<i>P. admetoides</i> Warén & Ponder, 1991	Florida Escarpment, seep.	624–631	GM	Recent	more spiral keels on body-whorl, and also notably large number of axial ribs, up to 34–45 according to Warén and Ponder (1991), which make it most distinct from all <i>Provanna</i> species
<i>P. annae</i> Nekhaev, 2023	Plip Volcano, Bering Sea, vent.	387–342	NP	Recent	lack the strong angulation
<i>P. beebei</i> Linse et al., 2019	Beebe Chimlets, Beebe Vent Field, Mid-Cayman Spreading Centre, vent.	4956–4972	CS	Recent	more number of spiral ribs and less strong axial ribs
<i>P. buccinoides</i> Warren & Bouchet, 1993	Hine Hina, Lau Basin; North Fiji Basin, vent.	1900–2765	WP	Recent	more angulation
<i>P. chevalieri</i> Warén & Bouchet, 2009	Regab site, West Africa, seep.	3150	WA	Recent	lack the shelf-structure
<i>P. cingulata</i> Chen, Watanabe & Ohara, 2016	the Shinkai Seep Field, Southern Mariana Forearc.	5687	WP	Recent	lacks angulation and axial sculpture, has an increasing number of spiral ribs
<i>P. clathrata</i> Sasaki et al., 2016	Irabu Knoll and Hatoma Knoll, Okinawa Trough, Japan, vent.	1647–1743	WP	Recent	more angulation and spiny, no tubercles, and lacks the shelf-structure
<i>P. cooki</i> Linse et al., 2019	East Scotia Ridge segment E9, Southern Ocean, vent.	2394–2641	SO	Recent	higher whorls and lacks tubercles
<i>P. exquisita</i> Chen & Watanabe, 2022	Eifuku Volcano, Mariana Arc,	1606	WP	Recent	more angulation to form spiral keels
<i>P. fenestrata</i> Chen, Watanabe & Sasaki, 2019	Crane site, Tarama Hill, Okinawa Trough, Japan, vent.	1559	WP	Recent	strong axial and spiral sculptures, raised and equally spaced

Species of <i>Provanna</i>	Distribution and Environment	Buried/survival depth (m)	Ocean/Area*	Age	Morphological comparison to <i>P. dongshaensis</i> sp. nov.
<i>P. glabra</i> Okutani, Tsuchida & Fujikura, 1992	off Hatsushima, Sagami Bay, Japan, seep.	1110–1200	WP	Recent	lack the strong angulation
<i>P. goniata</i> Warén & Bouchet, 1986	Guaymans Basin, seep.	2000–2020	EP	Recent	more angulation and spiny
<i>P. ios</i> Warén & Bouchet, 1986	East Pacific Rise 21°N–17°S, Galapagos Spreading Center, vent.	2450–2620	EP	Recent	more angulation, spiny, and higher spiral shell
<i>P. kuroshimensis</i> Sasaki et al., 2016	Kuroshima Knoll, Okinawa, Japan, seep.	644	WP	Recent	lack the strong angulation
<i>P. laevis</i> Warén & Ponder, 1991	Gulf of California, Guaymas Basin, Oregon Margin, Juan de Fuca Ridge, vent and seep.	500–2000	EP	Recent	lack the strong angulation
<i>P. lomana</i> Warén & Bouchet, 1986	Oregon Margin, seep.	450–1200	EP	Recent	lack the strong angulation, and the spiral ribs on the body-whorl
<i>P. lucida</i> Sasaki et al., 2016	Minami-Ensei Knoll, Okinawa Trough, Japan, vent.	701	WP	Recent	lack the strong angulation
<i>P. macleani</i> Warén & Bouchet, 1989	Oregon Margin, seep and sunken drift wood.	2713–2750	EP	Recent	more number of spiral ribs and less strong axial ribs
<i>P. muricata</i> Warén & Bouchet, 1986	East Pacific Rise 21°N, Galapagos Spreading Center, and North Fiji and Lau Back-Arc Basins, vent.	2450–2615	EP	Recent	more angulation and spiny
<i>P. nassariaeformis</i> Okutani, 1990	Mariana Back-Arc Basin, Manus Back-Arc Basins, vent.	3670–3680	WP	Recent	more number of axial ribs and lack the shelf-structure
<i>P. pacifica</i> Warén & Bouchet, 1986	Gulf of Panama; Oregon Margin; Costa Rica Margin	1017–2750	EP	Recent	more angulation and spiny
<i>P. reticulata</i> Warén & Bouchet, 2009	Regab, Guinness and MPS 1-Congo sites, West Africa, seep.	750–3150	WA	Recent	more angulation and spiny, more number of spiral ribs
<i>P. sculpta</i> Warén & Ponder, 1991	Louisiana Slope, seep.	550	GM	Recent	similar strong and swollen tubercles at the intersections between spiral and axial ribs, but lack the shelf-structure; and higher spiral shell
<i>P. segonzaci</i> Warén & Ponder, 1991	Lau Back-Arc Basin, vent.	1750–1900	WP	Recent	more angulation, spiny, and lack the shelf-structure
<i>P. shinkaiae</i> Okutani & Fujikura, 2002	Japan Trench, seep.	5343	WP	Recent	more angulation and spiny, higher spiral shell
<i>P. stephanos</i> Chen, Watanabe & Sasaki, 2019	‘Off Hatsushima’ seep site, Sagami Bay, central Honshu, Japan, seep.	908	WP	Recent	major spines on the spiral ribs and more angulation to form spiral keels
<i>P. subglabra</i> Sasaki et al., 2016	Okinawa Trough, Japan, vent.	710–1632	WP	Recent	lack the strong angulation
<i>P. variabilis</i> Warén & Bouchet, 1986	Juan de Fuca Ridge, Endeavour Segment, Gorda Ridge, Oregon Margin, vent, seep.	675–2200	EP	Recent	less strong axial ribs and lack the shelf-structure

†: fossil record.
*Abbreviation of ocean/area: CS, Caribbean Sea; EP, East Pacific; GM, Gulf of Mexico; NP, North Pacific; SA, South America; SO, Southern Ocean; WP, West Pacific; WA, West Africa.

and *P. macleani* have the comparable sculpture with numerous spiral ribs, whereas *P. dongshaensis* sp. nov. has a lesser number of spiral ribs but more prominent axial structure. The shelf-structure, characterized by significant angulation, appears in the *P. dongshaensis* sp. nov., but is absent in *P. buccinoides*, *P. clathrata*, *P. nakagawaensis*.

Especially the emergence of bead-like tubercles in *P. dongshaensis* sp. nov. seems to be a unique trait only shared with one extant species (*P. sculpta*) living in the

Gulf of Mexico and Caribbean Sea, far from SCS. The new fossil species *P. dongshaensis* sp. nov. can therefore be quickly distinguished from other species that are angulate and spiny, such as *P. goniata*, *P. ios*, *P. pacifica*, *P. muricata*, *P. reticulata*, *P. segonzaci*, *P. shinkaiae*, and *P. stephanos*. Another similar species, *Provanna fortis*, shares some features with *P. dongshaensis* sp. nov., including pronounced angulation, 2 spiral ribs on the spiral base and up to 5 on the lowermost whorl, and a

shelf-structure, etc. However, it features less robust axial structures on the body whorl with no indication of inflated tubercles or bead-like strings.

Shell microstructures of *Provanna*

The observation of shell microstructures was used as supplemental evidences for elucidation of the fossil vent and seep gastropods since they lost the organic body. According to the important report of microstructure related to provannid gastropods by Kiel (2004), the shell of modern species *Provanna variabilis* Warén & Bouchet, 1986 was composed of three layers of microstructure: an outer thin simple prismatic layer (oSPL), a thicker central complex crossed lamellar layer (CCL) and a thin inner simple prismatic layer (iSPL). Then more fossil material was subsequently investigated by Kiel (2006), Saether et al. (2010), and Amano and Little (2014). Based on the similarity of the shell microstructure between modern and fossil materials, together with observation of fossil abyssochrysoidean gastropod *Hokkaidoconcha hikidai* Kaim, Jenkins & Warén, 2008 from the Cretaceous seep sites in Hokkaido, the presence of an outer prismatic microstructural layer

and an underlying crossed lamellar microstructural layer is regarded as a common feature in the shells of all *Provanna* species, as well as in other provannid genera and in the Superfamily Abyssochrysoidea (Amano and Little 2014).

In *P. dongshaensis* sp. nov., the central complex crossed lamellar layer is markedly found in the SEM and present at all sections of the shell (Fig. 3A–D). The outer prismatic layer can be also found above the thicker crossed lamellar layer in *P. dongshaensis* sp. nov. (Fig. 3A, B, D), but seems to be thinner than that reported in other *Provanna* species (less than 20 μm surrounding the broken aperture). Similar to *P. marshalli*, the boundary or the transition between the outer simple prismatic and complex crossed lamellar layers of *P. dongshaensis* sp. nov. could be blurred and indistinct (Fig. 3A, D, also see Saether et al. 2010). However, there is a relatively obvious border between the inner simple prismatic layer and complex crossed lamellar layer at all observed positions of the shell (Fig. 3C, D). According to Saether et al. (2010) and Amano and Little (2014), the inner simple prismatic layer could be absent owing to the diagenesis processes, but it is present in *P. dongshaensis* sp. nov., similar to the case in *P. variabilis*, and look to be thicker than those in *P. reticulata* and *P. alexi*.

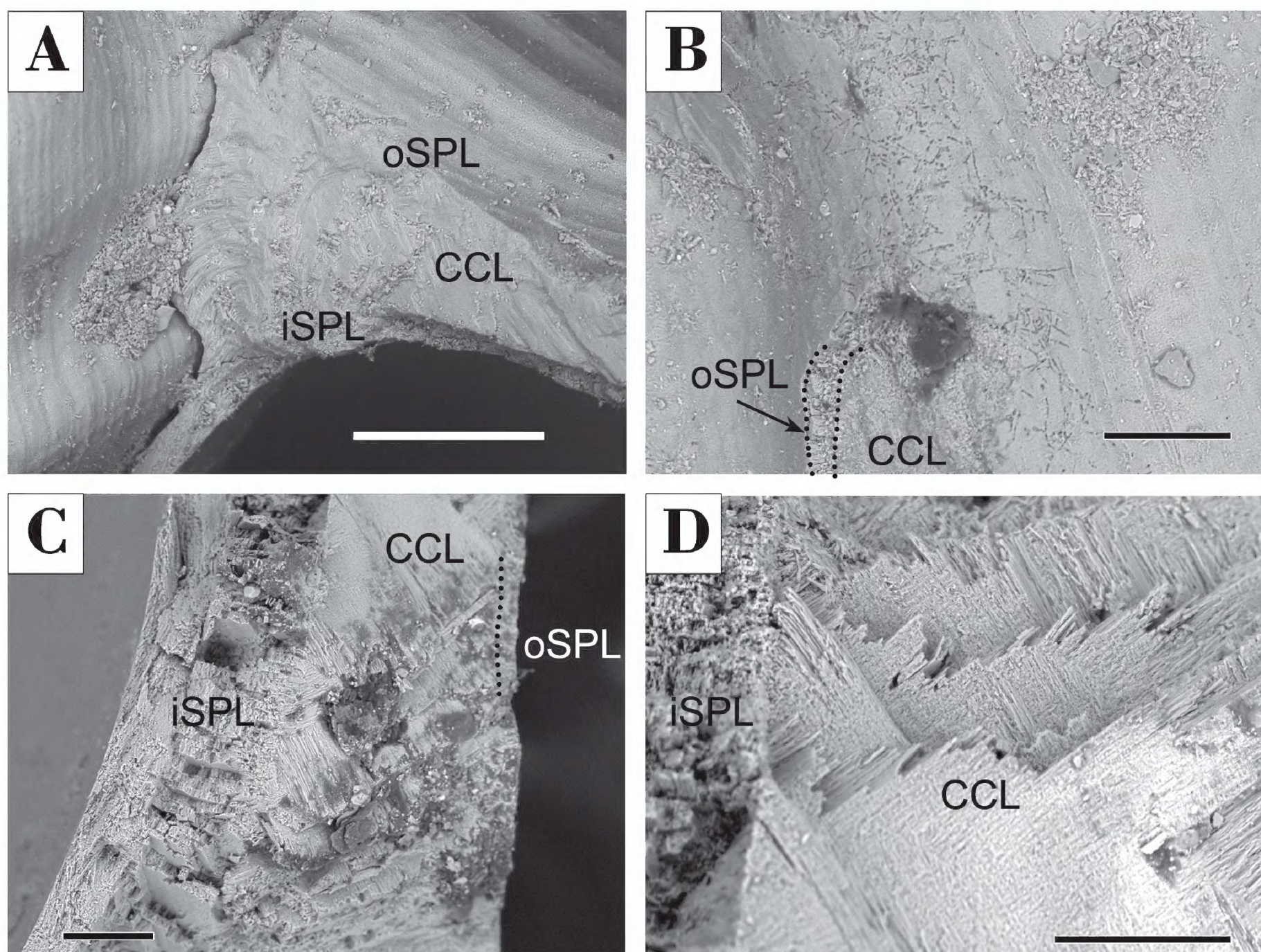


Figure 3. Shell microstructures of *Provanna dongshaensis* sp. nov. observed in SEM. **A.** Marginal exposure of specimen GMGS2-09B-C13; **B.** Eroded surface of specimen GMGS2-09B-C13; **C, D.** Marginal exposure of specimen GMGS2-09B-C14. Abbreviations: oSPL = outer simple prismatic layer; CCL = complex crossed lamellar layer; iSPL = inner simple prismatic layer. Scale bar: 200 μm (**A**), 100 μm (**B**), 50 μm (**C**), 30 μm (**D**).

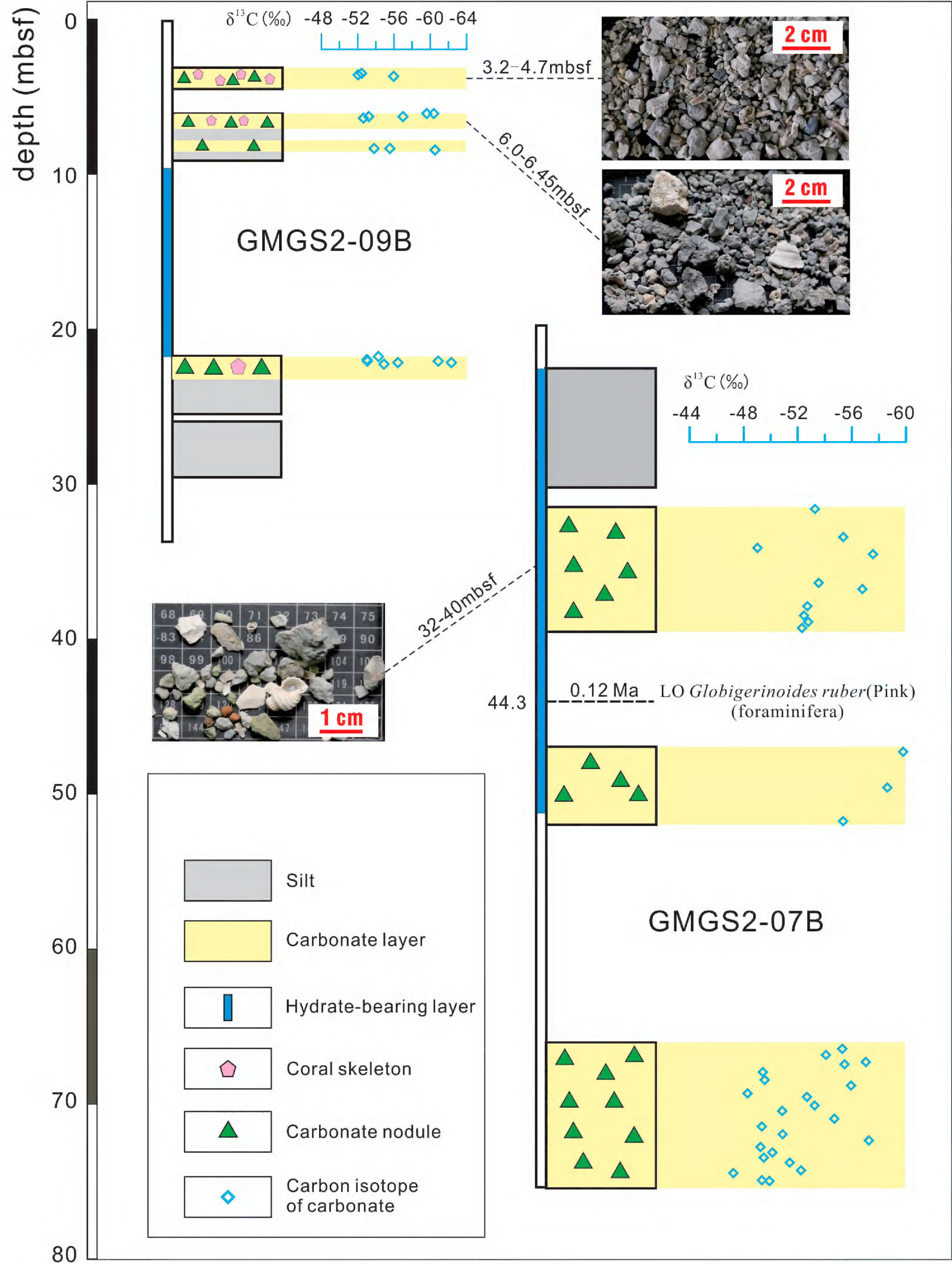


Figure 4. Three buried depths of *Provanna dongshaensis* sp. nov. distributed in the GMGS2-07B and GMGS2-09B with their lithology and remarkable negative carbon isotope values.

Buried depth, age and geological significance of *P. dongshaensis* sp. nov. in SCS

P. dongshaensis sp. nov. were yielded at the depth of 3.50, 3.60, 6.07 mbsf in GMGS2-09B and 33.85 mbsf in GMGS2-07B (Table 1, Fig. 4). At all these depths carbonate nodules were also yielded (Fig. 4). The stable carbon isotope signature ($\delta^{13}\text{C}_{\text{carbonate}}$) of the carbonate reveals significant negative values varied from about -48‰ to -62‰ (unpublished data, partly given in Fig. 4). The $\delta^{13}\text{C}_{\text{carbonate}}$ signature along with the petrography imply that these carbonate blocks developed at an ancient methane seep (Campbell 2006; Zhuang et al. 2016; Chen et al. 2016b). Such authigenic carbonate is considered as the product of methane hydrate dissociation via microbial anaerobic oxidation of methane in this area (Chen et al. 2016b, 2017). The age of two carbonate layers of GMGS2-09B which yield *P. dongshaensis* sp. nov. are late Pleistocene according to the AMS ^{14}C dating data of related coral skeleton (unpublished, also see Table 1). The *P. dongshaensis* sp. nov. buried at 33.85 mbsf in GMGS2-07B is also attributed to Pleistocene based on the last occurrence (LO) of foraminifera *Globigerinoides ruber* (pink) at the depth of 44.3 mbsf.

At the burial depths of the genus *Provanna*, a diverse assemblage of other gastropod species has also been identified. These species belong to the genus *Pusia* (Family Costellariidae), *Canidia* (Superfamily Buccinoidea), *Epitonium* (Family Epitoniidae) and *Lissotesta* (Family Ske-neidae) (data to be published). The occurrence of these gastropod fossils is closely correlated to the distribution of carbonate nodules, validating the inference that the beddings containing carbonate nodules in the study area are indicative of paleo-seepage activity across different phases/epochs. These episodic paleo-seepage events had created environments that were conducive to the growth and development of benthic organisms, particularly gastropod species.

Considering the adaption and endemic distribution, the discovery of provannid gastropods and accurate identification of *P. dongshaensis* sp. nov. could be the biological evidence, and play an essential role in explaining the existence of the ancient seep in the northern SCS during the Pleistocene. To date, *P. dongshaensis* sp. nov. is the only known *Provanna* fossil record in this hydrate-yielded location and in the Pleistocene epoch, expanding the geological range of genus *Provanna* geographically and temporally. To further understand and interpret the evolutionary history of genus *Provanna*, additional real fossil specimens should be gathered and examined in the future.

Furthermore, the carbonate nodules creating carbonate layers have widespread appearance in the neighboring drilling cores of this area, (e.g., at least 13 unique carbonate layers were recognized in GMGS2-08, Chen et al. 2016b). Some other gastropod specimens like

Neolepetopsidae have also been collected among these products of methane hydrate dissociation, and urgently need further accurate investigations in the near future. We suspect that there might be a significantly higher diversity of gastropods that persisted around the ancient hydrocarbon seep in the northern SCS. Such buried-seep sedimentary samples of GMGS2 series drilling cores could represent enlarged materials for systematic research of deep-sea gastropods and other chemosynthesis fauna.

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References

- Amano K, Jenkins RG (2013) A new species of *Provanna* (Gastropoda: Provannidae) from an Oligocene seep deposit in eastern Hokkaido, Japan. *Paleontological Research* 17: 325–329. <https://doi.org/10.2517/1342-8144-17.4.325>
- Amano K, Little CTS (2014) Miocene abyssochrysoid gastropod *Provanna* from Japanese seep and whale-fall sites. *Acta Palaeontologica Polonica* 59: 163–172. <https://doi.org/10.4202/app.2012.0002>
- Bettters MJ, Cordes EE (2023) New records of *Provanna* (Gastropoda, Provannidae) from the Costa Rica Margin and an identification key for the genus. *ZooKeys* 1189: 1. <https://doi.org/10.3897/zookeys.1189.109734>
- Campbell KA (2006) Hydrocarbon seep and hydrothermal vent paleoenvironments and paleontology: Past developments and future research directions. *Palaeogeography, Palaeoclimatology, Palaeoecology* 232: 362–407. <https://doi.org/10.1016/j.palaeo.2005.06.018>
- Chen C, Watanabe HK (2022) A new provannid snail (Gastropoda, Abyssochrysoidea) discovered from Northwest Eifuku Volcano, Mariana Arc. *ZooKeys* 1112: 123. <https://doi.org/10.3897/zookeys.1112.85950>
- Chen DF, Huang YY, Yuan XL, M CIL (2005) Seep carbonates and preserved methane oxidizing archaea and sulfate reducing bacteria fossils suggest recent gas venting on the seafloor in the Northeastern South China Sea. *Marine and petroleum Geology* 22: 613–621. <https://doi.org/10.1016/j.marpetgeo.2005.05.002>
- Chen C, Watanabe HK, Ohara Y (2016a) A very deep *Provanna* (Gastropoda: Abyssochrysoidea) discovered from the Shinkai Seep Field, Southern Mariana Forearc. *Journal of the Marine Biological Association of the United Kingdom* 98: 439–447. <https://doi.org/10.1017/S0025315416001648>
- Chen F, Lu H, Liu J, Zhuang C, Wu C, Cao J, Zhou Y, Liu G (2016b) Sedimentary geochemical response to gas hydrate episodic release on the northeastern slope of the South China Sea. *Earth Science (in Chinese)* 41: 1619–1629.

- Chen F, Zhou Y, Wu C, Liu J, Su X, Zhuang C, Lu H, Yu S, Duan X, Jin X (2017) Records and timing of gas hydrate and cold seep activity during the Last Glacial Period from the east of the Pearl River Mouth Basin, the South China Sea. *Earth Science Frontiers* 24: 66–77.
- Chen C, Watanabe HK, Sasaki T (2019) Four new deep-sea provannid snails (Gastropoda: Abysochrysoidea) discovered from hydrocarbon seep and hydrothermal vents in Japan. *Royal Society open science* 6: 190393. <https://doi.org/10.1098/rsos.190393>
- Feng D, Qiu J, Hu Y, Peckmann J, Guan H, Tong H, Chen C, Chen J, Gong S, Li N (2018) Cold seep systems in the South China Sea: An overview. *Journal of Asian Earth Sciences* 168: 3–16. <https://doi.org/10.1016/j.jseaes.2018.09.021>
- Gill FL, Harding IC, Little CTS, Todd JA (2005) Palaeogene and Neogene cold seep communities in Barbados, Trinidad and Venezuela: An overview. *Palaeogeography Palaeoclimatology Palaeoecology* 227: 191–209. <https://doi.org/10.1016/j.palaeo.2005.04.024>
- Hybertsen F, Kiel S (2018) A middle Eocene seep deposit with silicified fauna from the Humptulips Formation in western Washington State, USA. *Acta Palaeontologica Polonica* 63: 751–768. <https://doi.org/10.4202/app.00525.2018>
- Johnson S, Warén A, Lee R, Kano Y, Kaim A, Davis A, Strong E, Vrijenhoek R (2010) Rubyspira, new genus and two new species of bone-eating deep-sea snails with ancient habits. *The Biological Bulletin* 219: 166–177. <https://doi.org/10.1086/BBLv219n2p166>
- Kaim A, Jenkins RG, Warén A (2008) Provannid and provannid-like gastropods from the Late Cretaceous cold seeps of Hokkaido (Japan) and the fossil record of the Provannidae (Gastropoda: Abysochrysoidea). *Zoological Journal of the Linnean Society* 154: 421–436. <https://doi.org/10.1111/j.1096-3642.2008.00431.x>
- Kaim A, Jenkins RG, Hikida Y (2009) Gastropods from Late Cretaceous Omagari and Yasukawa hydrocarbon seep deposits in the Nakagawa area, Hokkaido, Japan. *Acta Palaeontologica Polonica* 54: 463–490. <https://doi.org/10.4202/app.2009.0042>
- Kiel S (2004) Shell structures of selected gastropods from hydrothermal vents and seeps. *Malacologia-Philadelphia* 46: 169–184.
- Kiel S (2006) New records and species of molluscs from Tertiary cold-seep carbonates in Washington State, USA. *Journal of Paleontology* 80: 121–137. [https://doi.org/10.1666/0022-3360\(2006\)080\[0121:NRASOM\]2.0.CO;2](https://doi.org/10.1666/0022-3360(2006)080[0121:NRASOM]2.0.CO;2)
- Kiel S, Hansen BT (2015) Cenozoic methane-seep faunas of the Caribbean region. *PLoS One* 10: e0140788. <https://doi.org/10.1371/journal.pone.0140788>
- Kiel S, Hybertsen F, Hyzny M, Klompmaker AA (2020) Mollusks and a crustacean from early Oligocene methane-seep deposits in the Talara Basin, northern Peru. *Acta Palaeontologica Polonica* 65: 109–138. <https://doi.org/10.4202/app.00631.2019>
- Linse K, Nye V, Copley JT, Chen C (2019) On the systematics and ecology of two new species of *Provanna* (Gastropoda: Provannidae) from deep-sea hydrothermal vents in the Caribbean Sea and Southern Ocean. *Journal of Molluscan Studies*: 1–14. <https://doi.org/10.1093/mollus/eyz024>
- Nekhaev IO (2023) Who lives in the hot heart of the cold sea? A new species of *Provanna* (Caenogastropoda: Provannidae) from the Hydrothermal zone of Piip Volcano, Northwestern Pacific. *Diversity* 15: 581. <https://doi.org/10.3390/d15040581>
- Ogura T, Watanabe HK, Chen C, Sasaki T, Kojima S, Ishibashi J-i, Fujikura K (2018) Population history of deep-sea vent and seep *Provanna* snails (Mollusca: Abysochrysoidea) in the northwestern Pacific. *PeerJ* 6: e5673. <https://doi.org/10.7717/peerj.5673>
- Okutani T (1990) Two new species of *Provanna* (Gastropoda: Cerithiacea) from “snail pit” in the hydrothermal vent site at the Mariana Back-Arc Basin. *Venus (Japanese Journal of Malacology)* 49: 19–24.
- Okutani T, Fujikura K (2002) Abyssal gastropods and bivalves collected by Shinkai 6500 on slope of the Japan Trench. *Venus (Journal of the Malacological Society of Japan)* 60: 211–224.
- Okutani T, Tsuchida E, Fujikura K (1992) Five bathyal gastropods living within or near the Calyptogena-community of the Hatsushima Islet, Sagami Bay. *Venus (Japanese Journal of Malacology)* 51: 137–148.
- Saether KP, Little CTS, Campbell KA (2010) A new fossil provannid gastropod from Miocene hydrocarbon seep deposits, East Coast Basin, North Island, New Zealand. *Acta Palaeontologica Polonica* 55: 507–517. <https://doi.org/10.4202/app.2009.1112>
- Sasaki T, Warén A, Kano Y, Okutani T, Fujikura K (2010) Gastropods from recent hot vents and cold seeps: systematics, diversity and life strategies. In: Kiel S (Eds) *The Vent and Seep Biota. Topics in Geobiology*, vol 33. Springer, Dordrecht, 169–254. https://doi.org/10.1007/978-90-481-9572-5_7
- Sasaki T, Ogura T, Watanabe HK, Fujikura K (2016) Four new species of *Provanna* (Gastropoda: Provannidae) from vents and a seep off Nansei-shoto area, southwestern Japan. *Venus* 74: 1–17.
- Sibuet M, Olu K (1998) Biogeography, biodiversity and fluid dependence of deep-sea cold-seep communities at active and passive margins. *Deep Sea Research Part II: Topical Studies in Oceanography* 45: 517–567. [https://doi.org/10.1016/S0967-0645\(97\)00074-X](https://doi.org/10.1016/S0967-0645(97)00074-X)
- Warén A, Bouchet P (1986) Four new species of *Provanna* Dall (Prosobranchia, Cerithiacea?) from East Pacific hydrothermal sites. *Zoologica Scripta* 15: 157–164. <https://doi.org/10.1111/j.1463-6409.1986.tb00218.x>
- Warén A, Bouchet P (1989) New gastropods from East Pacific hydrothermal vents. *Zoologica Scripta* 18: 67–102. <https://doi.org/10.1111/j.1463-6409.1989.tb00124.x>
- Warén A, Bouchet P (1993) New records, species, genera, and a new family of gastropods from hydrothermal vents and hydrocarbon seeps. *Zoologica Scripta* 22: 1–90. <https://doi.org/10.1111/j.1463-6409.1993.tb00342.x>
- Warén A, Bouchet P (2009) New gastropods from deep-sea hydrocarbon seeps off West Africa. *Deep Sea Research Part II: Topical Studies in Oceanography* 56: 2326–2349. <https://doi.org/10.1016/j.dsr2.2009.04.013>
- Warén A, Ponder WF (1991) New species, anatomy, and systematic position of the hydrothermal vent and hydrocarbon seep gastropod family Provannidae fam. n. (Caenogastropoda). *Zoologica Scripta* 20: 27–56. <https://doi.org/10.1111/j.1463-6409.1991.tb00273.x>
- Zhuang C, Chen F, Cheng S, Lu H, Wu C, Cao J, Duan X (2016) Light carbon isotope events of foraminifera attributed to methane release from gas hydrates on the continental slope, northeastern South China Sea. *Science China Earth Sciences* 59: 1981–1995. <https://doi.org/10.1007/s11430-016-5323-7>